

CHARACTERISTICS OF EGG-LAYING AND EGGS OF YEARLING PHEASANTS

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AMONG populations of wild pheasants (*Phasianus colchicus*) which have become established in the United States it is not uncommon for two or more females to deposit eggs in the same nest. These communal nests, commonly called "dump nests," may contain from 20 to 50 eggs (Baskett, 1947:10; Stokes, 1954:27; Dale, 1956:23). A communal nest is ordinarily identified as such by measuring the rate of egg deposition in the nest. It is impossible to determine whether two or more hens are laying in the same nest if the nest is not under surveillance during the egg-laying period.

Usually, dump nests are abandoned voluntarily by the hens; Stokes (1954:33) reported that less than 25 per cent of clutches of 20 eggs or more were incubated, whereas about 60 per cent of clutches containing between 5 and 16 eggs were incubated. Investigations of the nesting ecology of wild pheasants in east-central Illinois during 1957-61 revealed that 57 of 127 nests (45 per cent) that were voluntarily abandoned by the hen, or hens, and 37 of 133 nests (28 per cent) that had hatched, contained eggs of at least two distinctly different colors (R. F. Labisky, unpublished data). These findings of differently colored eggs in nests suggested to us that (1) communal laying might be a factor causing the abandonment of many nests other than the obvious dump nests and (2) two or more hens might be contributing to successful clutches that are normally attributed to single pheasant hens.

The objective of this research was to examine egg-laying and egg characteristics of pheasants, and to determine whether the stability of shell color or size of eggs (or both) laid by individual pheasants was a satisfactory criterion for identifying the number of hens contributing eggs to single nests in the wild.

METHODS

Nine pen-reared hen pheasants, approximately 10 months old, were obtained from the Illinois State Game Farm, Mt. Vernon, and transported to Urbana on 20 March 1964. These hens will be referred to as yearlings in this paper. The hens were held as a group in a large outdoor pen until they were individually caged, prior to the onset of laying, on 10 April. The individual cages, 51 × 56

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PLATE 1. Shell color of 98 of the 107 eggs laid by hen 334 (Fig. 3), 1964. Eggs presented in the chronological order in which they were laid, with the first egg shown at the left of the top row. Eggs No. 52, 69, 88, 92, 98, 101, 104, 105 (third from last egg), and 107 (last egg) not photographed. This color plate sponsored by the Illinois Natural History Survey.

× 33 cm in size, were situated in an outdoor battery. Between 20 March and 9 April the hens were fed a ration of mixed grain, supplemented with oyster shells; prior to 20 March the hens had been fed a commercial maintenance ration. From 10 April through the conclusion of the experiment each hen was fed an exclusive diet of Purina Game Bird Layena and water ad libitum. The weight of the nine hens averaged $1,026 \pm 23(\text{SE})\text{g}$ on 27 April 1964.

The eggs were collected each evening and measured within 48 hours. All eggs were weighed on a Shadowgraph balance to the nearest 0.1 g and measured (maximum length and width) to the nearest 0.1 mm with vernier calipers. Shell color was determined by matching each egg with the most similar color as presented by Maerz and Paul (1950). All color determinations were made under uniform fluorescent lighting.

In discussing color according to the system of Maerz and Paul (1950), the following terms must be defined. *Hue* is the name of the color. *Purity* represents the amount of gray added to a color to reduce its reflective ability, i.e., as increasing amounts of gray are added, the color will approach black. *Strength* refers to the intensity of color; the full strength of a hue at each level of purity is reduced in strength (or neutralized) to no hue by adding increasing amounts of white or gray.

Maerz and Paul divided color, consistent with the spectrum, into seven major groups: red to orange; orange to yellow; yellow to green; green to blue-green; blue-green to blue; blue to red; and purple to red. Each group is represented by eight successive color plates. The first plate of each group is presented in full purity, whereas the following seven plates show decreasing purity, i.e., progressively increasing amounts of gray. Plates 1 through 8, for each major color group, reflected 86, 74, 67, 48, 38, 28, 20, and 10 per cent of light, respectively; the eight plates are numbered 9-16 for the orange to yellow group, 17-24 for the yellow to green group, and 25-32 for the green to blue-green group. Each plate is divided into 12 rows (numbered 1-12) and 12 columns (lettered A to L). Each group has a total of 23 analogous hues corresponding to the squares in the far right column (L) and in the bottom row (12); in the orange to yellow group, for example, the hues grade from orange in the lower left corner of the plate, to yellow-orange in the lower right corner, and to yellow in the upper right corner of the plate. Each hue, at a specific level of purity, is expressed in 12 degrees of strength, grading from full strength at the terminal position to no hue at the upper left corner of the plate. Thus, on the first plate of each group (full purity) the hues reduce to white (no hue), whereas on the other seven plates of the group the hues reduce to neutral grays (no hue). Each color group is, descriptively, a 3-dimensional color model.

In order to express eggshell color, we have described it according to the number, letter, and plate system of Maerz and Paul. The use of this system will allow the reader, with the aid of Maerz and Paul (1950), to observe the actual variations in shell color that occurred among the eggs. A numerical system was derived so that variations in shell color could also be expressed mathematically.

In this paper, the shell color of all eggs laid by each individual hen is presented in a 3-axis model, consisting of x , y , and z axes centered on a midpoint which represents the mean shell color. The x axis represents the

horizontal variation (rows) and the y axis, the vertical variation (columns) in egg color according to the Maerz and Paul system; thus, both the x and y axes correspond essentially to strength of hues. The z axis represents variation from plate to plate of a particular color group, corresponding to purity. A fourth parameter, the c axis, is used to describe the variations in shell color of those eggs of individual hens that fell into two or more major color groups. All eggs laid by hens in this experiment were included within three major color groups: orange to yellow; yellow to green; and green to blue-green.

Our designation of egg color refers to any detectable color difference among different eggs, whether this difference be in hue, strength, purity, or color group.

RESULTS

The egg-laying cycle.—The few published findings on the reproductive physiology of the pheasant, an indeterminate egg-layer according to the criterion of Cole (1917:505), suggest that the mechanisms of ovulation and oviposition are similar, although not identical, to those of the domestic fowl (*Gallus gallus*). The reader is referred to Nalbandov (1959a and 1961) and Fraps (1961) for discussions of the physiological mechanisms controlling ovulation and oviposition in birds, particularly domestic fowl. The domestic hen, subjected to optimal photoperiods (12–14 hours of light), typically lays an egg on each of 2 or more consecutive days, does not lay on 1 day, and lays again on 2 or more consecutive days (Fraps, 1961:134). The egg, following ovulation, usually spends about 25–26 hours in the oviduct (mostly in the shell gland) prior to oviposition, and ovulation of the subsequent egg does not occur until 30–60 minutes after oviposition of the previous egg. Usually a hen does not ovulate after 3 P.M. Thus, each day, ovulation among a series of consecutive eggs becomes successively later until a scheduled ovulation falls late in the afternoon and is held in abeyance, which accounts for failure of the hen to lay the next day (Nalbandov, 1958:116). In this paper, the number of eggs laid by a hen on consecutive days is termed a *sequence*, and the number of days between oviposition of the terminal egg in one sequence and the initial egg in the following sequence is termed a *lapse*.

The first egg of the laying season from the nine yearling pheasants studied at Urbana (Lat. 40°N) was laid between 7–10 April, the last on 24 August (Table 1). Kabat and Thompson (1963:121) reported that yearling hens confined in pens near Madison, Wisconsin (Lat. 43°N) commenced laying on 13 April in 1949. The initiation of egg-laying by yearling, or first-year, pheasant hens usually lags several days behind that of old, or adult, hens (Kabat and Thompson, 1963:121; Westerskov, 1956:56).

TABLE 1
CHARACTERISTICS OF EGG-LAYING OF NINE YEARLING PHEASANTS, URBANA, ILLINOIS, 1964

| Hen | Date of | | Total number of eggs laid | Days in laying period | Rate of laying | | Total number | Sequences | | Total number | Lapses | |
|-------|-------------|----------|---------------------------|-----------------------|----------------|----------|--------------|-------------------|-------|--------------|-----------|-------|
| | First egg * | Last egg | | | Days per egg | Per cent | | Eggs per sequence | Range | | Mean | Range |
| | | | | | | | | | | | | |
| 334 | 12 April | 24 Aug. | 107† | 135 | 1.26 | 79 | 18 | 5.9 | 1-49 | 17 | 1.7 | 1-4 |
| 335 | 11 April | 11 June | 47 | 62 | 1.31 | 76 | 15 | 3.1 | 1-7 | 14 | 1.1 | 1-2 |
| 336 | 12 May | 24 June | 19 | 44 | 2.32 | 43 | 10 | 1.9 | 1-7 | 9 | 2.8 | 1-6 |
| 337 | 11 April | 8 July | 78 | 89 | 1.14 | 88 | 9 | 8.7 | 1-41 | 8 | 1.4 | 1-2 |
| 340 | 11 April | 16 July | 84 | 97 | 1.15 | 87 | 14 | 6.0 | 1-23 | 13 | 1.0 | 0 |
| 342 | 11 April | 16 Aug. | 104 | 128 | 1.23 | 81 | 22 | 4.7 | 1-11 | 21 | 1.1 | 1-3 |
| 343 | 12 April | 8 July | 65 | 88 | 1.35 | 74 | 22 | 3.0 | 1-7 | 21 | 1.1 | 1-2 |
| 344 | 13 April | 24 July | 88 | 103 | 1.17 | 85 | 14 | 6.3 | 1-24 | 13 | 1.2 | 1-2 |
| 345 | 18 April | 24 June | 43 | 68 | 1.58 | 63 | 21 | 2.1 | 1-5 | 20 | 1.3 | 1-3 |
| Total | | | 635 | 814 | | | 145 | | | 136 | | |
| Mean | 16 April | 11 July | 70.6 (9.8)‡ | 90.4 (9.9) | 1.28 | 78 | 16.1 (1.6) | 4.4 (0.5) | | 15.1 (1.6) | 1.3 (0.1) | |

* Three eggs were laid by the nine hens between 7-10 April. The first egg of the season was laid on 5 April by a yearling hen not included in this experiment.

† Egg breakage occurred in the cage of hen 334; shell color was determined on only 102 eggs, shell measurements on 99 eggs, and weights on 98 eggs.

‡ Numbers in parentheses are standard errors of means.

Egg production by the nine yearlings averaged 70.6 eggs for the season, with extremes of 19 and 107 eggs; the laying period averaged 90.4 days in length, with extremes of 44 and 135 days (Table 1). These findings substantiated those of Westerskov (1956:77), who reported that 37 yearling Ring-necked Pheasants (*Phasianus colchicus torquatus*), confined at Ngon-gotha, New Zealand (Lat. 38°S) averaged 67.3 eggs during a single laying season. The age of the hen apparently affects egg production, as Kabat and Thompson (1963:121) and Westerskov (1956:77) observed yearling pheasant hens to lay fewer eggs than older hens. However, among domestic fowl, Romanoff and Romanoff (1941:11) reported that egg production is heaviest among pullets and then declines throughout the life of the hen. Evidence obtained by Buss, Meyer, and Kabat (1951:41) in Wisconsin indicated that wild pheasant hens often laid as many as 55 per season, and that hens from wild populations and from artificially propagated stock commenced laying at about the same time in April. Thus, the average pheasant hen in a wild population retains egg-laying capabilities for a period of at least 3 months each breeding season, which explains its persistent ability

TABLE 2
FREQUENCY OF SEQUENCES CONTAINING DIFFERENT NUMBERS OF EGGS LAID BY NINE
YEARLING PHEASANTS, URBANA, ILLINOIS, 1964

| Number of eggs per sequence | Frequency of sequences | | Eggs contributed | |
|-----------------------------------|------------------------|----------|------------------|----------|
| | Number | Per cent | Number | Per cent |
| 1 | 42 | 29 | 42 | 7 |
| 2 | 23 | 16 | 46 | 7 |
| 3 | 23 | 16 | 69 | 11 |
| 4 | 16 | 11 | 64 | 10 |
| 5 | 14 | 10 | 70 | 11 |
| 6 | 5 | 3 | 30 | 5 |
| 7 | 6 | 4 | 42 | 7 |
| 8 | 2 | 1 | 16 | 3 |
| 9 | 2 | 1 | 18 | 3 |
| 10 | 3 | 2 | 30 | 5 |
| 11 | 2 | 1 | 22 | 3 |
| 12 | 1 | <1 | 12 | 2 |
| 18 | 1 | <1 | 18 | 3 |
| 19 | 1 | <1 | 19 | 3 |
| 23 | 1 | <1 | 23 | 4 |
| 24 | 1 | <1 | 24 | 4 |
| 41 | 1 | <1 | 41 | 6 |
| 49 | 1 | <1 | 49 | 8 |
| Total | 145 | 100 | 635 | 102 |

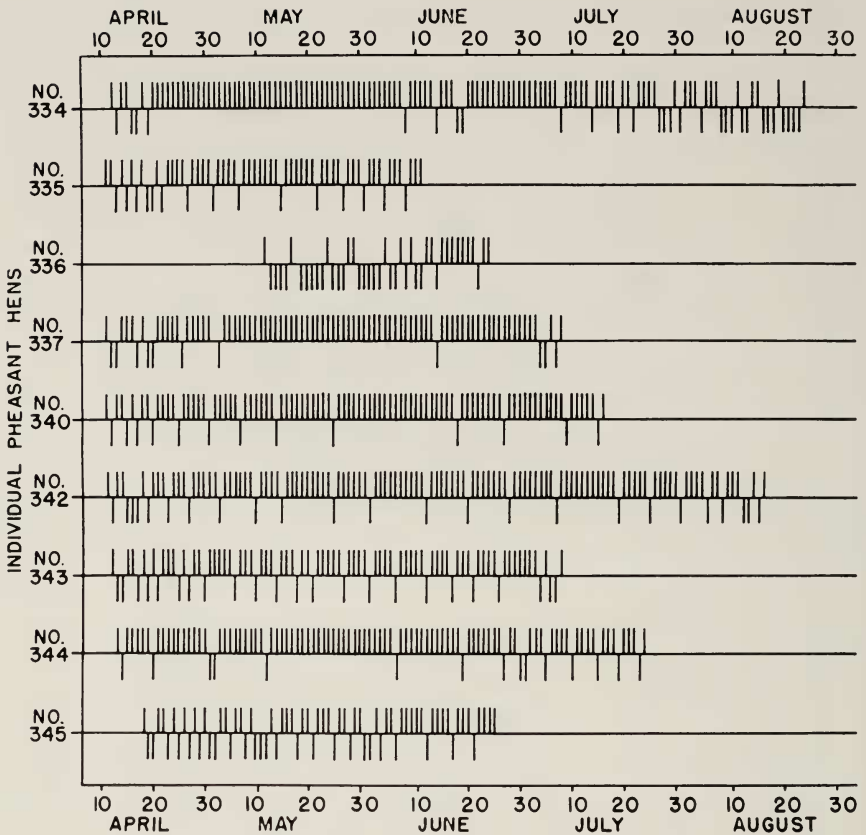


FIG. 1. Distribution of egg sequences and days of lapse during the complete seasonal laying cycle of nine yearling pheasants, 1964. Bars above the lines indicate number of eggs laid on consecutive days (sequence); bars below the lines indicate number of days "skipped" between successive eggs (lapse).

to renest following the disruption of one or more previously established, but not hatched, nests (Seubert, 1952; Warnock and Joselyn, 1964).

The seasonal rate of laying for the nine hens ranged from a low of 43 per cent (2.32 days per egg) to a high of 88 per cent (1.14 days per egg), and averaged 78 per cent (1.28 days per egg) (Table 1). A similar mean rate of laying among captive pheasants, 1.3 days per egg, was reported by Buss et al. (1951:35). Greeley (1962:188) also found a rate of laying of 1.3 days per egg among pheasants on diets containing at least 2 per cent calcium; Greeley's study was terminated on 5 June, prior to the end of the laying season. Monthly rates of laying for the yearlings in this study

averaged 70 per cent in April, 81 per cent in May, 84 per cent in June, 78 per cent in July, and 58 per cent in August. The occurrence of the best rates of laying, in May and June, coincided well with the major period of nest establishment of wild pheasants in east-central Illinois (R. F. Labisky, unpublished data).

The numbers of sequences of eggs laid by the nine yearlings averaged 16.1, with an average of 4.4 eggs per sequence (Table 1). The longest sequence contained 49 eggs. Sequences containing 1 to 5 eggs comprised 81 per cent of all sequences and contributed 46 per cent of all eggs (Table 2).

The average lapse between successive sequences was 1.3 days, with extremes of 1 and 6 days (Table 1). Single-day lapses comprised 81 per cent of all lapses. Hen 340 exhibited single-day lapses throughout her laying period (Fig. 1). Many of the deviations from single-day lapses, particularly for certain hens, occurred either early or late in the egg-laying period.

An egg-laying *rhythm* comprised of irregular sequences and irregular lapses was most common, occurring among eight of the nine hens; sequences were characteristically longer than lapses (Fig. 1). The egg laying of hen 340 was, however, characterized by irregular sequences and regular lapses (single-day lapses). The long sequences of hens 334 and 337, 49 and 41 eggs, respectively, indicated that successive ovulations occurred regularly at approximately 24-hour intervals. The variability of rhythm between sequences and lapses for these young hens evinces an irregularity in timing of successive ovulations which may be associated with all pheasant hens, or associated predominantly with yearling hens, or may be caused by the experimental conditions.

Eggshell characteristics and color.—Shell color of bird eggs, the physiology of which is largely under genetic control, is due to a combination of porphyrins and bile pigments; the bile pigments (biliverdin and bilirubin) arise as products of the catabolism of the porphyrin of hemoglobin. The red-brown pigment of the eggshell is oöporphyrin (protoporphyrin), which is present in the brown eggshells of domestic fowl and in the eggshells of many other species, including the pheasant (*Phasianus [colchicus] torquatus*) and some passerine birds (Fisher and Kögl, 1923:261; Völker, 1942:279). Oöcyan, a blue or blue-green pigment considered identical to biliverdin, has been extracted from the eggshells of gulls and other wild birds (Lemberg, 1931:90). Tixier (1945:631) extracted two bilin pigments from the green egg of the Emu (*Dromiceius novaehollandiae*); one pigment was biliverdin (or oöcyan), and the other very likely bilirubin.

According to the classic concept of the mechanisms of eggshell coloration, the bile pigments are transported by the blood to the uterus (shell gland), from which they are excreted by glands of the uterine mucosa into the lumen of

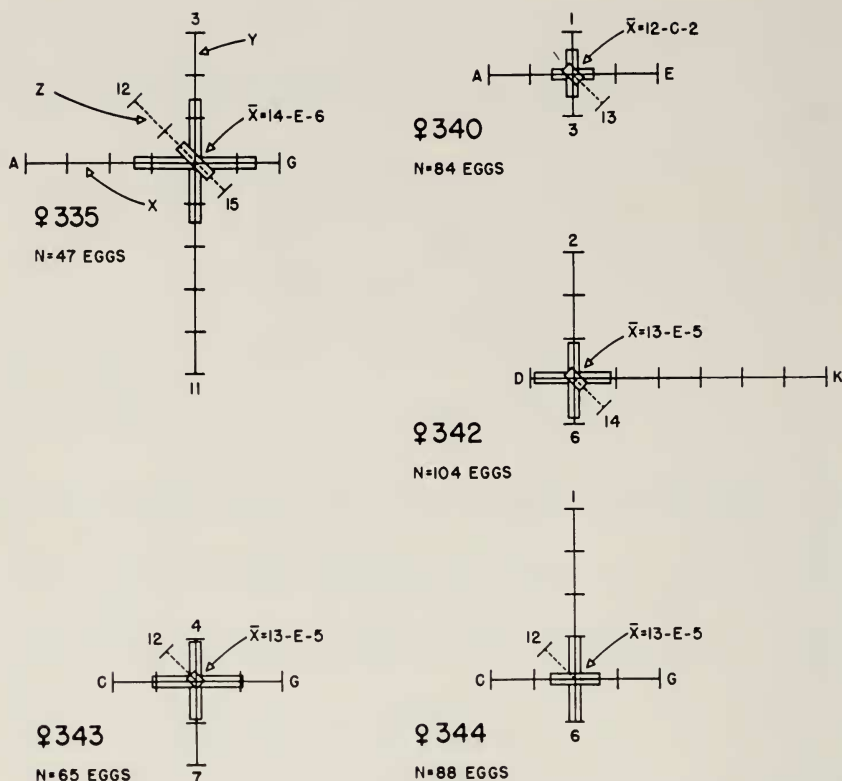
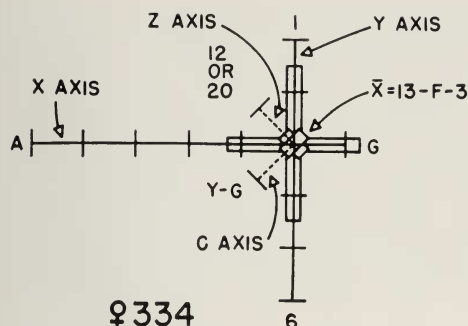
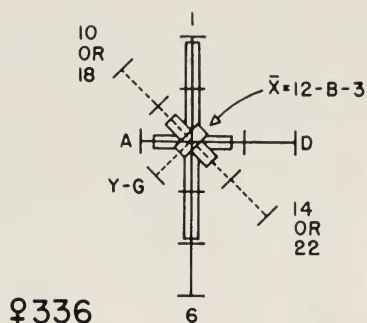


FIG. 2. Individual variations in shell color of eggs laid by yearling pheasants, 1964. Shell color of all eggs fall within the orange to yellow color group. Means, ranges, and standard deviations (open bars) are expressed in units corresponding to Maerz and Paul (1950): z axis corresponds to plate numbers, y axis to columns on plates, and x axis to rows on plates. Example: mean shell color for 47 eggs of hen 335 is 14-E-6, which refers to Plate 14 (28 per cent light reflection), column E, and row 6 in the orange to yellow color group.

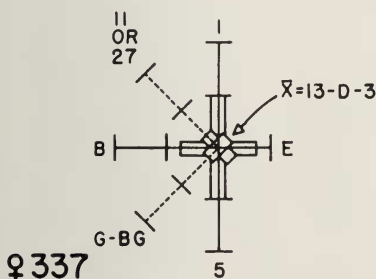
the uterus and are deposited on the eggshell (Romanoff and Romanoff, 1949: 227). This hemoglobin degradation cycle has not been proved, nor does it explain the presence of porphyrins in the shell (Polin, 1957:278). Polin (1957:277) reported that the uterus of the domestic hen was capable of forming porphyrins in vitro from delta-aminolevulinic acid, a known intermediate in porphyrin synthesis. He also found that uterine tissue from domestic hens that laid white eggs was as capable of in vitro porphyrin synthesis as the uterine tissue from hens that laid brown eggs. Polin (1957:278) thus suggested that eggshell color might be more dependent on the amount of



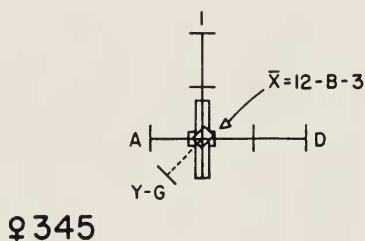
N (ORANGE TO YELLOW)=95 EGGS
N (YELLOW TO GREEN)=7 EGGS



N (ORANGE TO YELLOW)=17 EGGS
N (YELLOW TO GREEN)=2 EGGS



N (ORANGE TO YELLOW)=77 EGGS
N (GREEN TO BLUE-GREEN)=1 EGG



N (ORANGE TO YELLOW)=42 EGGS
N (YELLOW TO GREEN)=1 EGG

FIG. 3. Individual variations in shell color of eggs laid by yearling pheasants, 1964. Shell color of eggs of each hen is distributed between two color groups; the mean shell color for each hen falls within the orange to yellow color group. Means, ranges, and standard deviations (open bars) are expressed in units corresponding to Maerz and Paul (1950). *c* axis corresponds to color groups, *z* axis to plate numbers, *y* axis to columns on plates, and *x* axis to rows on plates. Example: mean shell color for 102 eggs of hen 334 is 13-F-3, which refers to Plate 13 (38 per cent light reflection), column F, and row 3 in the orange to yellow color group. See Plate 1 (frontispiece) for color photograph of eggs of hen 334.

aminolevulinic acid in the system of the hen than on the porphyrin-synthesizing ability of the uterus.

Among the nine yearling pheasants, eggshell color was found to be a variable characteristic among eggs laid by individual hens as well as among eggs laid by different hens (Plate 1 and Figs. 2 and 3). Shell color was most variable among eggs laid by hens 334 and 336 and least variable among eggs

laid by hen 340. Typically, the coloration of eggshells of pheasants consisted of a ground color without superficial markings (Plate 1), although occasional flecks of color, differing from the ground color, appeared on some eggs, particularly at the small end. Most of the eggs laid by these young hens were characterized by shells of a "smooth," glossy texture, indicating the presence of a uniformly deposited cuticle on the shell. However, five of the eggs laid by hen 334, all members of a 49-egg sequence, possessed shells with a rough or sandy texture (Plate 1). The penultimate egg in the 49-egg sequence of hen 334 was soft-shelled; this hen also laid a second soft-shelled egg near the completion of laying.

Among the 630 pheasant eggs for which shell color was determined, 619 (98 per cent) were confined to the orange to yellow color group, 10 to the yellow to green group, and 1 to the green to blue-green group. Shell color of the eggs laid by five of the nine hens remained exclusively within the yellow to orange color group (Fig. 2). No hens laid eggs whose shell color fell into more than two color groups (Fig. 3, *c* axis). Even among those hens whose eggs fell into two color groups, the majority of the eggshells were contained within the orange to yellow color group. One hen (not included in this experiment) laid eggs whose shell color was confined exclusively to the green to blue-green color group. The shell color of eggs laid by wild pheasants is probably most commonly, though not exclusively, associated with the orange to yellow color group.

The color values along the *x* and *y* axes (Figs. 2 and 3) yielded a combined measure of hue, and its strength; hue represented the pigment responsible for eggshell "color" within any specific color group. The mean values of the *x* and *y* axes for the 630 eggs were represented by E and 4, respectively, which revealed that hue was expressed at about 75 per cent of full strength.

Purity of color, along the *z* axis, measured the concentration of the eggshell pigment in terms of reflected light. Among the 630 eggs, 422 (67 per cent) and 161 eggs (26 per cent) were grouped at levels of purity with light-reflecting capabilities of 38 and 48 per cent, respectively.

Changes occurred in the shell color of eggs laid throughout the laying cycle, but were most obvious at the beginning and end of laying (Fig. 4). The shells of the first two, perhaps three, eggs were "lighter" in color than sub-

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FIG. 4. Comparisons of shell color, irrespective of color group, of the first five and last five eggs ($N=9$) with interim eggs ($N=540$) laid by nine yearling pheasants, 1964. The *x* and *y* axes represent hue, and its strength, and the *z* axis represents purity. Egg-shell colors become "darker" as the unit values of all axes increase. Horizontal lines indicate means; vertical lines, ranges; and open bars, standard deviations.

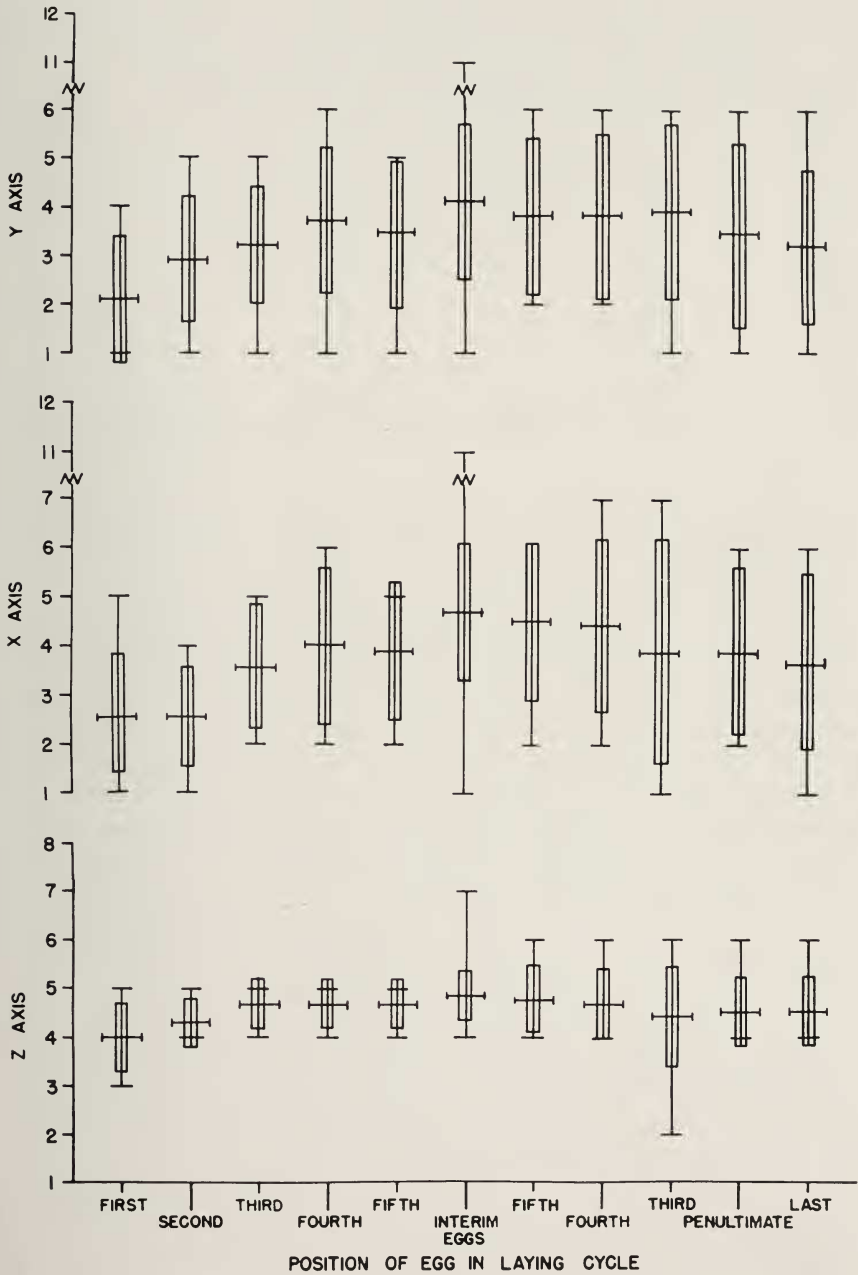


TABLE 3
FREQUENCY OF OCCURRENCE OF EGGS WITH IDENTICAL SHELL COLOR LAID SUCCESSIVELY
BY NINE YEARLING PHEASANTS DURING THEIR LAYING CYCLES, 1964

| Hen | Occurrence of groups of consecutively laid eggs of identical shell color* | | | | | | | | | | | Total number of eggs laid |
|------------|---|------|------|-----|-----|-----|-----|-----|-----|-----|-----|---------------------------------|
| | Number of eggs per group | | | | | | | | | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11+ | |
| 334 | 55 | 7 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1† | 102 |
| 335 | 24 | 7 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 47 |
| 336 | 10 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 19 |
| 337 | 31 | 8 | 6 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 78 |
| 340 | 34 | 8 | 1 | 3 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 84 |
| 342 | 52 | 12 | 3 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 104 |
| 343 | 29 | 7 | 3 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 65 |
| 344 | 38 | 15 | 3 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 88 |
| 345 | 12 | 5 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 43 |
| Total eggs | 285 | 144 | 75 | 44 | 20 | 6 | 7 | 0 | 9 | 20 | 20 | 630 |
| Per cent | 45.2 | 22.9 | 11.9 | 6.9 | 3.2 | 1.0 | 1.1 | 0.0 | 1.4 | 3.2 | 3.2 | 100.0 |

* Irrespective of sequences

† 20 eggs in group.

sequent eggs. In contrast, domestic pullets produced their darkest eggs at the onset of laying (Axelsson, 1932:164). Also, the last two or three eggs laid by yearling pheasant hens were slightly "lighter" in color than the preceding eggs, exclusive of the first two or three eggs of the cycle. There was some evidence that a sufficient degree of variability existed in the shell color of the third from the last egg in the laying cycle to render it a positional indicator marking the approaching end of laying. Much of the overall variability in shell color of eggs laid by individual hens was attributed to variations in shell color that occurred early and late in the laying cycle.

There was no stability of shell color among eggs of sequences, regardless of the number of eggs per sequence. In fact, among all sequences of two or more eggs (Table 2), eggs of identical color were recorded for only four two-egg sequences, two three-egg sequences, and one ten-egg sequence.

Axelsson (1932:190) reported that domestic hens laid eggs with darker shells immediately following a pause in laying or during periods of infrequent laying. These characteristics of pigment deposition were not detectable among the eggs laid by yearling pheasants.

An examination of the shell color of eggs laid consecutively by the yearlings, irrespective of sequences, indicated that it was most unlikely that the hens could lay a clutch of 9-12 eggs (normally expected in wild populations; Stokes, 1954:27) of identical color (Table 3). Only three of the nine yearlings could

TABLE 4
WEIGHTS (g) OF EGGS LAID BY NINE YEARLING PHEASANTS, 1964

| Hen | Number of eggs | Mean weight (g)* | Standard deviation (g) | Standard error (g) | Coefficient of variation (per cent) |
|-------|----------------|------------------|------------------------|--------------------|-------------------------------------|
| 334 | 98 | 23.9 | 2.0 | 0.2 | 8.5 |
| 335 | 47 | 26.9 | 1.7 | 0.8 | 6.5 |
| 336 | 19 | 21.0 | 4.1 | 0.9 | 19.7 |
| 337 | 78 | 25.6 | 1.3 | 0.1 | 4.9 |
| 340 | 84 | 27.3 | 0.9 | 0.1 | 3.3 |
| 342 | 104 | 29.7 | 1.5 | 0.2 | 5.1 |
| 343 | 65 | 30.3 | 1.1 | 0.1 | 3.5 |
| 344 | 88 | 28.1 | 1.6 | 0.2 | 5.7 |
| 345 | 43 | 28.8 | 1.3 | 0.2 | 4.4 |
| Total | 626 | 27.3 | 2.9 | 0.1 | 10.5 |

* An analysis of variance of the differences among mean weights of eggs laid by individual hens yielded an F value of 163.76, which was statistically significant at the 0.01 level of probability; the reference F was 2.55 at 8 and 617 df.

have possibly, but not probably, deposited nine or more eggs of the same color in a nest during the laying season. Thus, because of its instability, shell color among eggs laid by individual hens (at least yearling hens) cannot be considered a reliable criterion for identifying the number of hens contributing to single nests in the wild.

The effect of environmental exposure on eggshell color was measured by placing 12 eggs of various known colors in each of four nests, two of which were placed in shaded sites and two in sites exposed directly to the sun. Shell color of these eggs was redetermined after periods of 10 and 20 days of natural exposure during June and July, 1964. Changes in shell color were negligible among eggs exposed in shaded sites. Shell color faded among eggs exposed directly to the sun, i.e., color was reduced in strength of hue and in purity; the fading of shell color was greater after 20 days than after 10 days of exposure and greater among the darker-colored than among the lighter-colored eggs. These findings suggest that shell color measured from eggs exposed in nests of birds in the wild may not be representative of true eggshell color.

Egg weights and dimensions.—The weights of eggs laid by individual yearlings were relatively stable, but statistically significant differences occurred among the mean weights of eggs laid by different hens (Table 4). There was no correlation between the total number and the mean weight of eggs laid by individual hens.

The mean weight of 626 eggs laid by the yearling pheasants was 27.3 g (Table 4). The heaviest egg recorded was 33.5 g and the lightest, 5.4 g; the latter egg did not contain a yolk. Romanoff and Romanoff (1949:62) re-

TABLE 5
COMPARISON OF THE MEAN WEIGHTS (G) OF THE FIRST TEN EGGS LAID WITH ALL
SUBSEQUENT EGGS, AND OF THE LAST TEN EGGS LAID WITH THE INTERIM EGGS.
ALL EGGS LAID BY YEARLING PHEASANTS, 1964

| Hen | Number of eggs | (μ_1) Mean weight of eggs 1-10 | (μ_2) Mean weight of subsequent eggs | Test of signifi- cance; $\mu_1 < \mu_2$ * | (μ_1') Mean weight of last 10 eggs | (μ_2') Mean weight of interim eggs† | Test of signifi- cance; $\mu_1' < \mu_2'$ * |
|-----|----------------------|---|--|--|---|--|--|
| 334 | 98 | 24.3 | 23.9 | ns | 22.9 | 24.0 | ns |
| 335 | 47 | 24.3 | 27.6 | s | 28.2 | 27.3 | ns |
| 337 | 78 | 24.3 | 25.8 | s | 24.9 | 26.0 | s |
| 340 | 84 | 26.7 | 27.4 | s | 27.3 | 27.4 | ns |
| 342 | 104 | 26.3 | 30.1 | s | 30.3 | 30.1 | ns |
| 343 | 65 | 29.4 | 30.5 | s | 30.3 | 30.6 | ns |
| 344 | 88 | 24.8 | 28.5 | s | 29.4 | 28.3 | ns |
| 345 | 43 | 27.4 | 29.3 | s | 29.8 | 29.1 | ns |

* Data tested by a one-tailed *t* test; s indicates statistical significance and ns indicates the lack of significance at the 0.05 level of probability.

† Interim eggs include all eggs except the first ten and last ten eggs laid by individual hens.

ported 32 g as a characteristic egg weight for pheasants, but did not specify the age or strain of the hens. Westerskov (1956:96) reported that 66 fresh eggs from a stock of pure Ring-necked Pheasants (*P. c. torquatus*) at the Urbana Game Farm, Ohio, averaged 32.1 g. Westerskov (1956:90) also found that among *P. c. torquatus* hens, artificially propagated in New Zealand, first-year breeders (yearlings) laid heavier eggs (32.9 g) than second-year breeders (31.0 g); the reverse was true among "Black-necked" Pheasants (*Phasianus c. colchicus*). The egg weights of pheasants recorded in this study are about 4-5 g per egg less than those reported by other workers. The influence of the small cages used to house the pheasants in this experiment seems inadequate to explain the smaller eggs, as Bailey, Quisenberry, and Taylor (1959:568) found that individually caged chickens produced heavier eggs than did floor-housed birds. Very likely, the reported differences in egg weights can be attributed to the genetic variability of the various stocks of pheasants.

In chickens, the first few eggs that a pullet lays are normally smaller than those laid subsequently in the laying period (Romanoff and Romanoff, 1949:73). The weights of eggs produced by the pheasants in this study followed a similar pattern. Among seven of eight hens (hen 336 excluded because of small sample), the mean weights of the first ten eggs of the laying period were significantly less than the mean weights of the eggs laid subsequently (Table 5). The mean weights of the last ten eggs were significantly less than the mean weights of the interim eggs for only one of the eight hens; in four hens, the mean weights of the terminal ten eggs were greater than those of the

TABLE 6

COMPARISON OF MEAN WEIGHTS (G) OF EGGS RELATIVE TO THEIR POSITION IN SEQUENCES OF ONE TO SIX EGGS. ALL EGGS LAID BY YEARLING PHEASANTS, 1964

| Number of eggs in sequence | Number of sequences | Position of egg in sequence | | | | | | Test of signifi- cance* |
|----------------------------------|---------------------------|-----------------------------|------|------|------|------|------|-------------------------------|
| | | 1 | 2 | 3 | 4 | 5 | 6 | |
| 1 | 41 | 25.6 | | | | | | |
| 2 | 21 | 26.7 | 26.8 | | | | | $t = 1.06$ ns |
| 3 | 21 | 28.2 | 28.1 | 28.0 | | | | $F = < 1$ ns |
| 4 | 14 | 28.8 | 29.7 | 28.9 | 28.8 | | | $F = < 1$ ns |
| 5 | 13 | 27.4 | 27.6 | 27.5 | 27.8 | 27.2 | | $F = < 1$ ns |
| 6 | 5 | 27.7 | 28.7 | 29.0 | 28.0 | 27.6 | 27.7 | $F = < 1$ ns |

* Test level was at 0.05 level of probability; ns indicates the lack of statistical significance.

interim eggs (Table 5). (Interim eggs include all eggs except the first ten and last ten laid by a hen.) Thus, among yearling pheasants, eggs apparently do not decrease in weight toward the end of the laying period.

Bennion and Warren (1933:363) concluded that in chickens, the first egg in a sequence was usually the largest, and that weights of succeeding eggs in the sequence decreased progressively. However, Tyler and Geake (1961:275) found this conclusion to be only partially applicable among two- and three-egg sequences, and not at all applicable among four- and five-egg sequences. In the Japanese Quail (*Coturnix c. japonica*), the first egg of the sequence was usually smaller, but not significantly so, than subsequent eggs (Woodard and Wilson, 1963:545). Kendeigh, Kramer, and Hamerstrom (1956:46) reported that the first egg of the clutch of the House Wren (*Troglodytes aedon*) was the smallest, but that a gradual increase in weight occurred among subsequent eggs of the clutch. Westerskov (1956:91) found that the first egg was lightest in clutches containing 12 or more pheasant eggs, and that each of the first six or seven eggs laid tended to be heavier than the preceding egg.

In this study, there were no significant differences in the mean weights of eggs at different positions in the sequences (Table 6). However, in the two-, four-, five-, and six-egg sequences, the first egg was lighter than the second egg.

There was no significant difference in the mean weight of eggs from sequences of different lengths laid by the yearling hens (Table 7), nor was there any apparent linear relationship between length of sequence and mean weight of eggs. This lack of relationship between sequence length and egg weight also exists in chickens (Tyler and Geake, 1961:275). However, in the House Wren, larger clutches contained heavier eggs (Kendeigh et al., 1956:64).

Mean width and mean length of 627 eggs laid by the yearling pheasants were 34.0 mm and 43.4 mm, respectively (Table 8). Romanoff and Romanoff

TABLE 7
MEAN ADJUSTED WEIGHTS (G) OF EGGS AS RELATED TO THE NUMBER OF EGGS PER SEQUENCE.* ALL EGGS LAID BY YEARLING PHEASANTS, 1964

| Number of eggs per sequence | Number of sequences | Mean adjusted weights (g)† |
|-----------------------------|---------------------|----------------------------|
| 1 | 41 | 20.0 |
| 2 | 21 | 20.2 |
| 3 | 21 | 20.1 |
| 4 | 14 | 20.6 |
| 5 | 13 | 20.7 |
| 6 | 5 | 21.3 |
| 7 | 6 | 21.4 |
| 8 | 2 | 21.8 |
| 9 | 2 | 21.1 |
| 10 | 3 | 20.7 |
| 11 | 2 | 21.2 |
| 12 | 1 | 21.5 |
| 19 | 1 | 20.8 |
| 23 | 1 | 21.0 |
| 24 | 1 | 21.0 |
| 41 | 1 | 21.5 |

* Weights were adjusted to eliminate bias among sequences of certain lengths that were not randomly distributed among the hens.

† An analysis of variance of the differences in the mean adjusted weights of eggs among different sequences yielded an *F* value of 1.16, which was not statistically significant at the 0.05 level of probability; the reference *F* was 1.67 at 15 and 528 df.

(1949:106) reported 35×44 mm as average dimensions for eggs from pheasants for which age and strain were not given. Westerskov (1956:90) reported that among *P. c. torquatus* hens, the eggs laid by first-year breeders averaged 35.8×45.9 mm, being very slightly larger than those laid by second-year breeders; however, among *P. c. colchicus* stock, yearling hens laid slightly smaller eggs than second-year hens. Both age and genetic constitution apparently influence egg size.

Although the variability among widths and among lengths of eggs laid by the yearlings was not great, statistically significant differences did exist among the mean widths and among the mean lengths of eggs laid by different hens (Table 8). In pheasants, as in domestic fowl (Romanoff and Romanoff, 1949:91), egg width was less variable than egg length.

Among the yearling pheasants, the first few eggs of the laying cycle were generally smaller than subsequent eggs. In seven of eight hens (hen 336 excluded because of small sample), either the mean width or the mean length of the first ten eggs laid was significantly less than of all subsequent eggs (Table 9). In three hens, both the mean width and mean length of the first ten eggs were significantly less than in subsequent eggs.

TABLE 8
MEAN MAXIMUM WIDTH (MM) AND MEAN MAXIMUM LENGTH (MM) OF EGGS LAID
BY NINE YEARLING PHEASANTS, 1964

| Hen | Num- ber of eggs | Width (mm) | | | | Length (mm) | | | |
|-------|---------------------------|------------|----------------------------|------------------------|---|-------------|----------------------------|------------------------|---|
| | | Mean* | Standard devia- tion | Stan- dard error | Coefficient of variation (per cent) | Mean* | Standard devia- tion | Stan- dard error | Coefficient of variation (per cent) |
| 334 | 99 | 32.6 | 0.97 | 0.10 | 3.0 | 45.5 | 1.57 | 0.16 | 3.4 |
| 335 | 47 | 33.9 | 0.74 | 0.11 | 2.2 | 42.4 | 1.33 | 0.19 | 3.1 |
| 336 | 19 | 30.9 | 3.12 | 0.72 | 10.1 | 38.7 | 4.25 | 0.97 | 11.0 |
| 337 | 78 | 33.6 | 1.15 | 0.13 | 3.4 | 42.0 | 1.03 | 0.01 | 2.5 |
| 340 | 84 | 33.9 | 0.37 | 0.04 | 1.1 | 44.0 | 0.88 | 0.10 | 2.0 |
| 342 | 104 | 34.8 | 0.53 | 0.05 | 1.5 | 45.5 | 1.56 | 0.15 | 3.4 |
| 343 | 65 | 35.4 | 0.49 | 0.06 | 1.4 | 44.3 | 0.82 | 0.10 | 1.9 |
| 344 | 88 | 34.7 | 0.62 | 0.06 | 1.8 | 42.9 | 1.21 | 0.13 | 2.8 |
| 345 | 43 | 34.7 | 0.63 | 0.10 | 1.8 | 44.7 | 1.05 | 0.16 | 2.3 |
| Total | 627 | 34.0 | 1.42 | 0.06 | 4.2 | 43.4 | 2.03 | 0.08 | 4.7 |

* An analysis of variance of the differences among mean diameters and among mean lengths of eggs laid by individual hens yielded *F* values of 126.03 and 80.90, respectively, which were statistically significant at the 0.01 level of probability; the reference *F* was 2.51 at 8 and 618 df.

A comparison of the three measurements of pheasant egg-size—weight, width, and length—revealed that egg-weight had the greatest coefficient of variation (10.5 per cent) and egg-width the lowest coefficient of variation (4.2 per cent). Yet, even variability among egg-widths was of sufficient magnitude to preclude egg-width as a criterion for accurately identifying the eggs laid by different yearling hens.

TABLE 9
COMPARISON OF MEAN MAXIMUM WIDTHS (MM) AND LENGTHS (MM) OF FIRST TEN EGGS
LAID WITH ALL SUBSEQUENT EGGS LAID BY YEARLING PHEASANTS, 1964

| Hen | (μ_1) Mean diameter of eggs 1-10 | (μ_2) Mean width of subse- quent eggs | Test of signifi- cance: $\mu_1 < \mu_2$ * | (μ_1') Mean length of eggs 1-10 | (μ_2') Mean length of subse- quent eggs | Test of signifi- cance: $\mu_1' < \mu_2'$ * |
|-----|---|--|---|--|--|---|
| 334 | 32.5 | 32.2 | ns | 42.9 | 42.5 | ns |
| 335 | 33.0 | 34.1 | s | 41.0 | 42.8 | s |
| 337 | 33.2 | 33.6 | ns | 41.1 | 42.2 | s |
| 340 | 34.1 | 33.9 | ns | 43.3 | 44.1 | s |
| 342 | 33.6 | 34.9 | s | 43.2 | 45.8 | s |
| 343 | 35.0 | 35.5 | s | 44.0 | 44.4 | ns |
| 344 | 33.9 | 34.9 | s | 41.0 | 43.2 | s |
| 345 | 34.0 | 34.9 | s | 44.8 | 44.7 | ns |

* Data tested by a one-tailed *t* test; s indicates statistical significance and ns indicates the lack of significance at the 0.05 level of probability.

DISCUSSION

Pheasants are "long-day" breeders, that is, their breeding activity is initiated by increasing photoperiods (Bissonnette and Csech, 1936:109). Among cock pheasants, the increasing day-length in spring causes a gradual rise in the gonadotrophin content of the pituitary, which is accompanied by an increase in testis weights and the attainment of spermatogenesis (Greeley and Meyer, 1953:353-354). Hen pheasants also show a gradual physiological achievement of full reproductive capacity in spring, but lag about a month behind cocks in attaining complete gametogenesis (Hiatt and Fisher, 1947: 538, 543).

Among domestic pullets, an increase in the size of the yolk (or ovum) is paralleled by an increase in total egg weight; the greatest gains in yolk size occur among eggs laid at the beginning of the laying season, after which time yolk size stabilizes (Romanoff and Romanoff, 1949:117-118). Assuming a parallelism between pheasants and pullets, the smallness of the first several eggs laid by yearling pheasants at the onset of laying, in contrast to eggs laid later in the cycle, may be partially the result of small yolks. Because the pituitary gonadotrophins, which govern follicular growth and ovulation among avian species (Nalbandov, 1958:117), strongly influence the size of the ova, we speculate that the gonadotrophins of yearling pheasants do not attain a level of maximum effectiveness until several eggs have been laid.

It seems plausible that the anatomical and glandular development of the oviduct, being dependent on estrogens, and progesterone or androgen (Nalbandov, 1959b:531), is also a gradual process. We postulate for yearling pheasants that the oviduct functions at a submaximal level at the time of the first ovulation in spring, and that it functions maximally only after the hen has experienced several ovulations. This postulate would serve to explain the gradual change from the lighter-colored eggs laid by yearling pheasant hens early in the laying cycle to the darker-colored eggs laid after the oviduct, particularly the shell gland, becomes "experienced." Apparently the secretory function of the shell gland of the oviduct of pheasants diminishes slightly near the termination of laying, i.e., onset of the refractory period, as evidenced by the reappearance of eggs with lighter-colored shells. That "inexperienced" oviducts, as well as small yolk sizes, may also contribute to the small size of the first several eggs laid by yearling pheasants is evidenced by our observations that eggs did not decrease in size at the end of the laying cycle.

SUMMARY

Egg production by nine yearling pheasants, maintained in captivity in 1964, averaged 70.6 eggs for the laying season, with extremes of 19 and 107; the laying season averaged 90.4 days in length, with extremes of 44 and 135. Rate of laying averaged 1.28 days per

egg per hen. The number of eggs laid by a hen on consecutive days (sequence) averaged 4.4. The lapse between successive sequences averaged 1.3 days; single-day lapses comprised 81 per cent of all lapses.

Shell color, a variable characteristic of eggs laid by and among individual hens, was confined predominantly to the orange to yellow color group. At least the first and last three eggs laid by yearling hens exhibited a "lighter" shell color than did the interim eggs.

The mean weight of eggs laid by yearling hens was 27.3 g, with average dimensions of 34.0×43.4 mm. Although the variability among weights and dimensions of eggs laid by individual hens was not great, significant variability in size did occur among eggs laid by different hens. Generally, the first ten eggs laid by yearlings were significantly smaller than subsequent eggs.

The variability in weight, width, length, and shell color of eggs laid by yearling pheasants was great enough to render these criteria insufficient for reliably segregating eggs laid by different hens in single nests in the wild.

The seasonal pattern of variations in shell color and size of eggs laid by yearling pheasants suggested that the level (or balance) of pituitary gonadotrophins and the function of the oviducts are submaximal at the time of first ovulation and that they become maximal only after the hens have experienced several ovulations.

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